

New Host and Distribution Records for *Leucospis* (Hymenoptera: Leucospidae) Associated Primarily with Nests of *Centris* (Hymenoptera: Anthophoridae) in the Dry Forests of Costa Rica

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Abstract.—A study conducted in the dry forests of Lomas Barbudal Biological Reserve, Guanacaste Province, Costa Rica, revealed new host records and elevation data for five species of *Leucospis*: *azteca*, *bulbiventris*, *cayennensis*, *egaia*, and *latifrons*. Four species of trap nesting *Centris* bees (Hymenoptera: Anthophoridae) were attacked, as well as at least 4 species of trap nesting bees in the family Megachilidae. Of 295 *Leucospis* wasps reared from these trap nesting bees, it was possible to associate 236 with hosts, 189 of which were from nests of *Centris bicornuta*. Elevational data and host species data are summarized for each *Leucospis* species reared, as well as sex ratios of reared material. Additional notes on biology and behavior are provided, along with a key to the five species reared from trap-nesting *Centris* bees in Costa Rica. The taxonomic status of *L. bulbiventris*, a sexually dimorphic species, is discussed relative to *L. manaica*.

Members of the family Leucospidae are among the largest species of Chalcidoidea, and all are parasitoids of solitary and subsocial aculeate bees and wasps. They drill through the hardened cell walls of their hosts' nests with their unusual ovipositors, and develop as ectoparasitoids. Excellent summaries of leucospid biology are provided by Clausen (1940), Habu (1962), and Bouček (1974). The family was revised on a world basis by Bouček (1974), who also summarized the known host data. Hosts were recorded for 32 of the 130 species of Leucospidae recognized by Bouček (1974). Prior to Bouček's (1974) revision, no species of leucospids had been recorded as parasitoids of *Centris* bees, though other anthophorids (notably species of *Xylocopa*) were known as hosts of at least three species of *Leucospis*. Subse-

quently, Chandler *et al.* (1985) reared two individuals of *L. cayennensis* Westwood from *Centris* in Minas Gerais, Brazil. Leucospids frequently parasitize megachilid bees in California (GWF, personal observations), and there are several published records of species of *Leucospis* attacking various megachilids (Bouček 1974, Burgis 1995).

Centris is a large genus of bees in the hymenopteran family Anthophoridae, with at least 32 species occurring in Costa Rica (Snelling, 1984). Their nesting habits are diverse. Some species make their nests in the ground while others utilize holes left in wood by other insects; some provision multiple cells per nest, others provision only one cell per nest. Aside from collecting pollen, all of them collect oil from plants that have oil producing flowers, and this oil is used in their nesting biology (Vinson *et al.* 1996).

Centris bees, because of their large size,

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are a readily observed component of the Mesoamerican dry forest habitat during the dry season. Trap-nests are very effective means of studying the activity of wood-cavity nesting species (Frankie *et al.* 1988, 1993, Vinson *et al.* 1996). In the area of this study, six species of *Centris* have been found to nest in tree holes, however only four of these are commonly found in the trap nests (Frankie *et al.* 1988). *Centris bicornuta* Mocsáry is one of the most abundant of the trap nesting species in this area (Frankie *et al.* 1988, 1993, 1997). A number of inquilines and parasitoids can be reared from trap-nests, and in the Guanacaste Province of Costa Rica, leucospids were one of the dominant parasitoids of some of the species of *Centris* being studied there. Below we record the first specific host associations for Leucospidae on *Centris* in Costa Rica.

MATERIALS AND METHODS

Study sites.—The study was conducted at the Lomas Barbudal Biological Reserve in the dry forest in Guanacaste Province, Costa Rica. Two bundles, each containing six block monitoring units (BMUs) (Frankie *et al.* 1993), were placed in dry forest sites at 100 m, 300 m, 600 m, and 800 m elevations in a transect extending from Hacienda Monteverde (at 100 m, 8 km NW Bagaces) northwards towards Volcan Rincón de la Vieja. All BMUs were hung at eye level on tree trunks in shaded locations, and were monitored at 14 day intervals throughout the dry season (late December to May). The 100 m site had a mixture of oak forest and riparian evergreen forest (Frankie *et al.* 1988), and had been disturbed by agricultural development. The 300–800 m sites were largely intact oak forest with several other scattered tree species. The oak species, *Quercus oleoides* Schlecht. & Cham., was the same at all four sites.

Trap nests.—The nesting activities of several species of *Centris* were monitored using BMUs. These BMUs consisted of 12

small wooden sticks ($11.5 \times 2.3 \times 2$ cm) with holes drilled in one end, bundled together to form a block. The wooden sticks (consisting of pine or two local hard wood species) were drilled lengthwise to a depth of between 7.0 to 11.0 cm depending on the hole sizes (diameters of 4.5, 6.5, 8, 9.5 and 11 mm were used). Two sticks representing each of the hole diameters, along with two additional sticks with a hole diameter of 8 mm, were bundled together using fine wire or twine. The 8 mm hole size was doubled as it is the hole size most commonly used by *Centris* bees (Frankie *et al.* 1988, 1993). Sticks were layered within the block so that a drilled end of a particular hole size always alternated with a non-drilled end, and small to large hole sizes descended from the top to bottom of a block.

Emergence.—Each BMU was numbered and identified as to location, altitude, and time and date of placement. Every 14 days the sticks with completed bee nests were replaced with a new stick of the same hole diameter and additional information was recorded on the removed stick, including date removed. Sticks with completed nests were placed in large wire baskets ($\sim 20 \times 20 \times 40$ cm) made of 2.5 cm open mesh hardware cloth that prevented access by mammals, but not parasitoids. These baskets were hung from nails on nearby trees. During the wet season, glass scintillation vials were taped to the nest entrances to intercept any emergences. Emergences were monitored on a two week basis and parasitoid and host associations recorded. Data presented here were collected during four consecutive years (December 1993 to December 1997).

Behavior and development.—All observations on female wasp behavior were made at 100 m sites where 2–4 BMUs were continuously being monitored. Completed nests, 1 to 14 days old, were removed from BMUs, placed in baskets at these sites, and observed daily during daylight hours for 3 weeks. Each basket contained

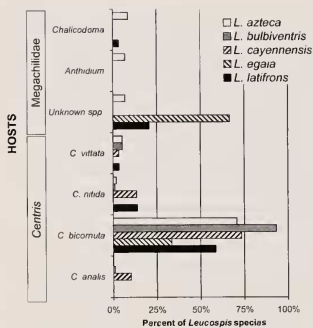


Fig. 1. Percent of each *Leucospis* species found on different hosts. Total for each *Leucospis* species across all hosts adds to 100%.

approximately 100 sticks arranged in three rows of two sticks deep so that each stick had at least one surface exposed. The number of leucospids searching or attempting to oviposit on nests was recorded until the experiment was terminated. One stick from each basket was removed daily during week 3 of the experiment, and opened to monitor bee development, and that of any present parasites, parasitoids, and diseases. This experiment was replicated 4 times.

Additional observations were made on 16 ovipositing female leucospids where, following completion of oviposition and departure of the leucospid, the exact drilling location was marked. The marked stick was then removed and dissected to determine the stage of the host attacked and the placement of the leucospid egg. Observations on oviposition behavior were also made on nests removed from BMUs and placed in baskets at the 100 m site.

Specimen repositories.—Voucher specimens for the *Centris* and megachilid bees are at University of California, Berkeley, and those for the *Leucospis* species are at

UC Berkeley and Texas A&M University (TAMU). Material for comparison, including primary types, was borrowed from the Philadelphia Academy of Natural Sciences (ANSP), the Natural History Museum, London (BMNH), and TAMU.

RESULTS AND DISCUSSION

Emergence data.—We reared 295 leucospids, representing five species, from at least seven species of wood-hole nesting bees in Guanacaste Province. Of 236 host bees, 189 were *Centris bicornuta* which was attacked by all five species of *Leucospis*: *L. azteca* Cresson, *L. bulbiventris* Cresson, *L. cayennensis* Westwood, *L. egaia* Walker, and *L. latifrons* Schletterer (Fig. 1). *Centris nitida* F. Smith and *C. vittata* Lepeletier each hosted four different species of *Leucospis* (Fig. 1). The most abundant leucospid in our samples was *L. bulbiventris* (56% of reared individuals) (Fig. 2). Discounting *L. egaia*, represented only by three reared individuals in our samples, all leucospids were more abundant at lower elevations (Fig. 3). *Leucospis azteca* and *L. cayennensis* were most abundant at the 100 m site; *L. bulbiventris* and *L. latifrons* were most abundant at the 300 m site (Fig. 3). In addition to *C. bicornuta*, *C. nitida*, and *C. vittata*, we also reared leucospids from *C. analis* F., undetermined species of *Chalicodoma* and *Anthidium* (Hymenoptera: Megachilidae), and at least two other undetermined species of megachilid bees, all from the trap nests described above.

The experimental environment employed in this study was artificial owing to the fact that the *Centris*-infested trap nests were highly accessible to leucospids by being clustered in baskets. The nests were thus at much higher densities than would be encountered in nature. In Costa Rican dry forests, *Centris* nests tend to be more widely dispersed, and the bees are not limited to nesting in holes in small sticks, which are maximally exposed for *Leucospis* oviposition. Therefore, the large number of leucospids recorded here is at

Frequency of Each *Leucospis* Species Reared

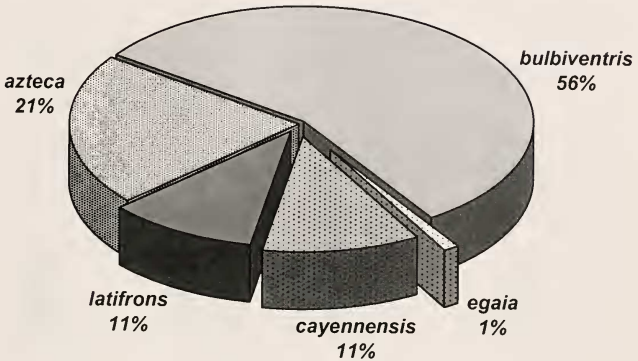


Fig. 2. Relative proportions of *Leucospis* species reared from trap nesting bees.

least in part a reflection of the experimental manipulations.

Observations on oviposition.—No female leucospids were observed around the wire baskets or on the sticks until nests were at least 3 weeks old (Fig. 4). Peak activity occurred towards the end of the third week, but since the experiment was terminated before all activity ceased, we lack data on how long nests remain attractive. Female leucospids fly up wind to the wire enclosures (100% $N = 19$), and ultimately land on one of the sticks containing bee nests. Generally, they walk the length of the stick slowly while alternately drumming the surface with their antennae. Prior to drilling, they stop to antennate the wood surface with both antennae held close together, then move forward half a body length to drill the antennated spot with the ovipositor.

Based on dissections of the 16 marked

cells into which leucospids were observed ovipositing, female leucospids only attacked cells in which the mature larvae had at least begun to spin a cocoon. Leucospid eggs were always located inside the cocoons, either on the surface of a host larvae still finishing its cocoon ($N = 1$), a prepupa ($N = 3$), or a pupa ($N = 12$). Of the 18 other leucospid larvae or pupae recorded from randomly dissected nests, all were within the cocoon of a bee, indicating that either the bee is allowed to develop to a prepupa and spin a cocoon, or they are only parasitized following cocoon formation. The failure to find leucospid larvae on younger stages of bee larvae, and the delay in leucospid response to newly provisioned bee nests, suggests that these leucospids, at least, do not attack earlier stages of their hosts. Parasitized host larvae did not move, but it was not clear if they

Proportions of Four Species of *Leucospis* Found at Different Elevations

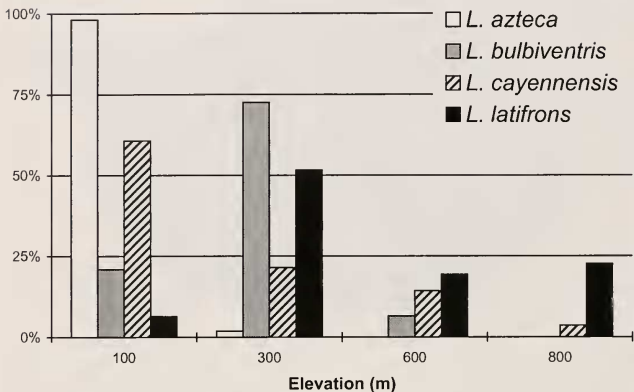


Fig. 3. Proportions of four species of *Leucospis* found at different elevations. Total for each *Leucospis* species across all elevations adds to 100%.

Average Number of *Leucospis* Attacks on Bee Nests

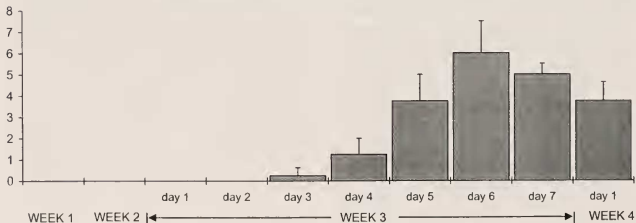


Fig. 4. Behavioral observations. Number of *Leucospis* attacks on provisioned sticks observed over time. Nests at the beginning of week 1 were from 1 to 14 days old. Observations were not extended beyond the first day of week 4.

were paralyzed since larvae at this stage of development are lethargic.

There have been few prior studies in which more than one species of leucospid has been reared from a single host species. In addition to the five specific examples listed by Bouček (1974), RAW (unpublished) has collected both *L. histrio* Maindron and *L. moleyreii* Maindron from nests of a single species of *Xylocopa* in Papua New Guinea. The data presented here represent the first record, to our knowledge, of five leucospid species reared from a single host species. Further, we know of only one species of Leucospidae previously associated with *Centris* bees (Fritz and Genise 1980, De Santis 1983, Chandler *et al.* 1985).

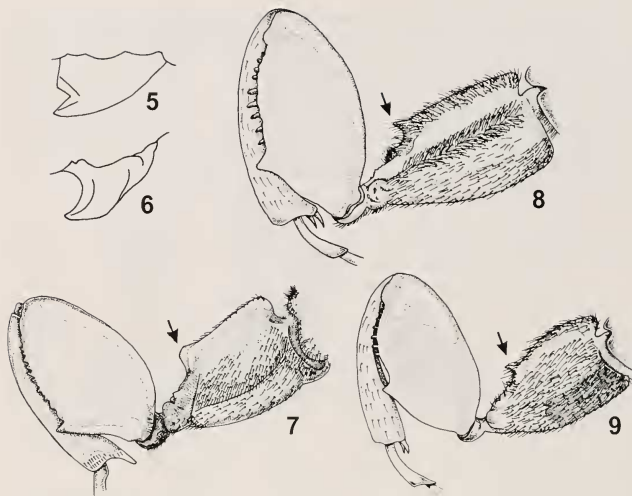
Parasitoid identifications.—Preliminary identifications of the *Leucospis* species were greatly facilitated by the excellent detail provided in the monograph by Bouček (1974). In our attempt to confirm the identifications of these species, however, we uncovered several problems as-

sociated with the primary types. The holotypes of *bulbiventris* and *dubiosa* Cresson and lectotype of *azteca* should be in ANSP. They were all examined by Bouček, and the types returned as indicated by correspondence at ANSP. Despite considerable effort by D. Azuma, however, no leucospid primary types could be found, though several others should also be at ANSP.

The key presented here to the leucospids attacking *Centris* bees in dry forests of Costa Rica is adapted largely from this work, as is the terminology. The key has been greatly simplified for ease in identification of leucospids attacking *Centris* in dry forests of Costa Rica, and should only be used in this context (or for comparison with *Centris* parasitoids from dry forests elsewhere). There are several other species of *Leucospis* known from Mesoamerica, and Bouček's work should therefore be consulted for any species not reared from *Centris*, and for rigorous confirmation of suspect individuals.

KEY TO SPECIES OF *LEUCOSPIS* ASSOCIATED WITH *CENTRIS* BEES IN COSTA RICAN DRY FOREST HABITATS

1. Pronotum with a transverse, premarginal cross carina and/or narrow yellow stripe near posterior margin. Mandible with triangular indentation on mesal chewing edge (Fig. 5) . . . 2
 - Pronotum without transverse, premarginal cross carina or narrow yellow stripe. Mandible with semicircular indentation on mesal, chewing edge (Fig. 6) . . . *L. cayennensis* Westwood
 2. Scutellum at least partly yellow 3
 - Scutellum completely without yellow coloration *L. bulbiventris* Cresson
 3. Hind femur with fewer than 10 small teeth on ventral margin. Hind coxa with a slender tooth (spine) on its dorsal posterior edge (as in Figs. 8, 9) 4
 - Hind femur with more than 10 small teeth on ventral margin. Hind coxa with a thin, partially translucent lobe on dorsal-posterior edge (as in Fig. 7), never with a spine-like tooth *L. egaia* Walker
 4. Setae on hind coxa converge towards center of depression (Fig. 8). Ovipositorial furrow on first metasomal tergum in the form of a simple, smooth, convex ridge down the midline (Fig. 11). Yellow coloration on scutellum restricted to posterior half, at least anterior half of scutellum black *L. latifrons* Schletterer
 - Setae on hind coxa nearly all pointing in the same direction, not converging towards the center (Fig. 9). Ovipositorial furrow on first metasomal tergum with a smooth, shiny, convex ridge down the midline, and concave slopes on either side of the ridge (Fig. 12). Nearly entire scutellum yellow or yellowish, with only anterior edge black *L. azteca* Cresson
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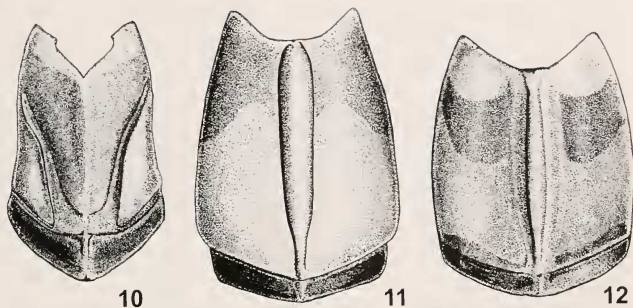


Figs. 5-9. Mandibles and hind legs of *Leucospis* species. 5. Mandible of *L. latifrons*, female. 6. Mandible of *L. cayennensis*, female. 7. Hind leg of *L. bulbiventris*, female. 8. Hind leg of *L. latifrons*, female. 9. Hind leg of *L. azteca*, female.

Leucospis azteca Cresson
(Figs. 9, 12)

Leucospis azteca, previously known only from the three specimens of the original type series, lacks obvious diagnostic features. It can be identified by the following combination of characters: mandible with triangular indentation (Fig. 5); pronotum with premarginal carina (a weak, transverse ridge within a yellow band that runs parallel and slightly anterior to the posterior margin of the pronotum), median lobe of metanotum (= dorsellum) coarsely sculptured, but without distinctly carinate lateral margins; hind tibia apically truncate; hind coxa regularly punctate and setose (as in Fig. 9); and ovipositorial furrow

as in Fig. 12. Bouček (1974) noted that *L. azteca* shared several features in common with both *L. latifrons* and *L. affinis* Say, and that the species had been variously confused in previous studies. *Leucospis latifrons* is readily identified by the pattern of dense pubescence on the hind coxa (compare Figs. 8 and 9), but one of the subspecies of *L. affinis* treated by Bouček, *L. a. dubiosa* Cresson, is particularly problematic as it is very similar to *L. azteca*. The apparent loss of the holotype of *L. azteca* and lectotype of *L. azteca* makes it even more difficult to separate *L. affinis* from *L. azteca*. Fortunately, the two other members of the original type series of *L. azteca* were located in ANSP. Structurally, both of



Figs. 10-12. Ovipositorial furrows on the first metasomal terga of *Leucospis* species. 10. *L. bulbiventris*, female. 11. *L. latifrons*, female. 12. *L. azteca*, female.

these agree very closely with our material, but there are some differences in color. This is particularly noticeable on the scutellum. In our material, the yellow coloration covers at least the posterior half of the scutellum, providing a readily observable field characteristic for separating this species from the otherwise similar *L. latifrons*. In both of the *L. azteca* paratypes, however, the scutellum is much less extensively yellow, and similar to our *latifrons* in this regard. Given this variation in color, we concur with Bouček (1974) that the differences in the ovipositorial furrow on the first metasomal tergum are important for distinguishing *L. affinis* from *L. azteca*, and it is on this basis that we have determined our material as *L. azteca*. In *L. azteca*, the furrow is generally not as deep as in *affinis* (a feature that is difficult to assess without side by side comparison), and scattered setae occur on the polished median ridge. In the specimens of *L. affinis* available to us from California and southern Texas, the median, polished ridge lacks setae (though these are abundant along the edge of the furrow). We have found that density of punctation on the

hind leg (a feature used by Bouček 1974) is too variable to be used for separation of *L. affinis*, *L. azteca*, and *L. latifrons* unless side by side comparison is possible with a good series of specimens representing all three species (which we were fortunate to have at our disposal).

The biology of this species was previously unknown. Our data suggest that it is a generalist, capable of attacking several different species. Of the 58 individuals for which we had host data, 41 came from *C. bicornuta*, 1 from *C. nitida*, 3 from *C. vittata*, 4 from *Anthidium*, 5 from *Chalicodoma*, and 4 from other undetermined species of Megachilidae. Unlike *L. latifrons*, *L. azteca* was confined to lower elevations. Of the 53 specimens for which we had altitudinal data, 98%, were reared from nests at 100 m, and only 2% from 300 m (Fig. 3). Of the 63 individuals we reared, only 17% were male, showing a strong female bias (Fig. 13). *Leucospis affinis* has been reared from a wide variety of megachilid bees, and could conceivably be found on the same hosts as *L. azteca* where their ranges overlap (e.g. in Mexico). As these species

are very difficult to separate, caution must be exercised when identifying them.

Leucospis bulbiventris Cresson
(Figs. 7, 10)

Leucospis bulbiventris is readily identifiable by the complete absence of yellow coloration on the scutellum, the shape of the ovipositorial furrow, which is exceptionally broad anteriorly (Fig. 10), the deep, triangular incision of the mandible (much deeper than in Fig. 5), and the shape of the hind coxa, which has a thin, partially translucent lobe on its dorsal posterior edge (Fig. 7). It is a large but slender species with a distinctly petiolate abdomen.

Leucospis bulbiventris was previously known only from the male holotype collected in Mexico. A second nominal species, *L. manaica* Roman, described from Brazil, has heretofore been known only from five females that are similar in many respects to the holotype of *L. bulbiventris* (Bouček 1974). We reared a good series of males and females, in several cases from the same host nest, enabling us to associate the sexes with certainty. Bouček (1974) was the first to suggest that perhaps *L. bulbiventris* and *L. manaica* represent different sexes of the same species. We confirm that the differences in setation and overall shape between *L. manaica* and *L. bulbiventris* noted by Bouček represent sexual dimorphism. Based on our rearings, we therefore strongly suspect that *L. manaica* and *L. bulbiventris* are the same; but because we do not have males from South America, and, more importantly, cannot locate the holotype of *L. bulbiventris*, we must unfortunately leave this problem unresolved. The name *bulbiventris* has priority over *manaica*, and since males from our material fit the description of *L. bulbiventris* provided by Bouček (1974), we have therefore used this name for our species.

No biological information has previously been published for either *L. bulbiventris* or *L. manaica*, nor have either of these been

recorded before from Costa Rica. Of the 116 individuals for which we have host data, the majority (108) came from nests of *C. bicornuta*. The others were reared from *C. analis* (1), *C. nitida* (1), and *C. vittata* (6). Of 150 reared individuals for which we have elevation data, 21% were from 100 m, 73% from 300 m, and only 7% from nests at 600 m. None were found at 800 m (Fig. 3). Of 165 individuals reared, only 19% were males, showing a strong female bias (Fig. 13).

Leucospis cayennensis Westwood
(Fig. 6)

This is a widespread Neotropical species recorded from Mexico to Argentina as well as the Caribbean (Fidalgo 1980, De Santis 1983). It is readily identified by the semicircular indentation of the mandible (Fig. 6), the complete lack of a transverse premarginal carina on the pronotum, and the relatively smooth hind coxa (with dorsal two-thirds of the depression smooth, shiny, bare and impunctate).

Fritz and Genise (1980) were the first to record *Centris tarsata* Smith as a host of *L. cayennensis*, and this is the only specific host recorded to date (Chandler *et al.* 1985, De Santis 1983). In Fritz and Genise's (1980) study, *L. cayennensis* was reared from 14% of the *C. tarsata* cells in old, abandoned *Sceliphron asiaticum* (L.) nests. Our data show that *L. cayennensis* attacks at least four other species of *Centris* bees. Of the 30 individuals for which we have host data, 22 came from nests of *C. bicornuta*, 4 from *C. nitida*, 3 from *C. analis*, and 1 from *C. vittata*. *Leucospis cayennensis* was found at all four elevations sampled during this study, but seemed to have a preference for lower elevations. Approximately 61% of the individuals for which we have elevational data were reared from nests at 100 m, 21% from 300 m, 14% from 600 m, and 4% from 800 m (Fig. 3). Of 33 individuals collected, one third were males, showing a female sex bias (Fig. 13).

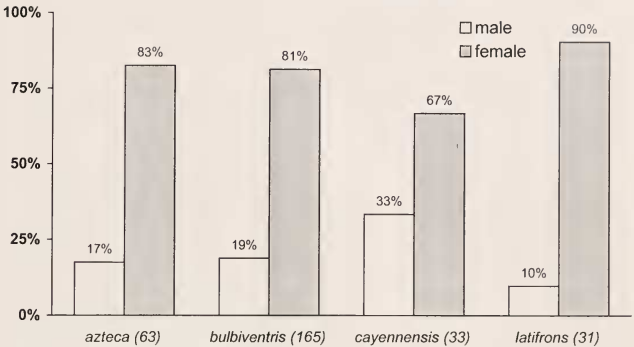
Sex Ratios for Reared *Leucospis* Species (N)

Fig. 13. Sex ratios of *Leucospis* species reared from trap-nesting hosts.

Leucospis egaia Walker

This species is similar in general appearance and coloration to *L. azteca* and *L. latifrons*, but has a carinately margined dorsellum, a more rounded, translucent lobe rather than a spinose tooth on the hind coxa, and an oblique rather than truncate margin to the hind tibia. No host records existed previously for *L. egaia* (Bouček 1974). We reared a male from *C. bicornuta* at 100 m, a male from a megachilid bee at 600 m, and a female from a megachilid bee at 600 m. Since only 3 individuals of this species were found, we cannot make general inferences about its biology.

Leucospis latifrons Schletterer (Figs. 5, 8, 11)

This is another widespread Neotropical species, occurring from Mexico to Bolivia. It is readily identified by the arrangement of the dense patch of setae in the central depression of the hind coxa (Fig. 8). The color pattern on the scutellum was sufficiently stable in our material to use for

separation of *L. azteca* from *L. latifrons* in the field. As noted above, however, these color patterns may vary from one locality to the next, and should be used cautiously for identification purposes. Hosts were previously unknown for *L. latifrons*. Of the 29 individuals for which we have rearing data, 17 came from *C. bicornuta*, 6 from megachilid bees, 4 from *C. nitida*, 1 from *C. vittata*, and 1 from *Chalicodoma*. Of the 32 individuals with altitudinal data, 6% came from nests at 100 m, 52% came from nests at 300 m, 19% from nests at 600 m, and 23% from nests at 800 m (Fig. 3). This species seems to be more of a generalist, able to adapt to a variety of hosts and elevations, with an apparent preference for habitats at 300 m. Although *L. latifrons* and *L. azteca* are extremely similar morphologically, the elevation data suggest a biological difference supporting Bouček's (1974) finding that they are two distinct species. Of 31 individuals reared, only 10% were male, showing a strong female bias, as in all the other species in our samples (Fig. 13).

ACKNOWLEDGMENTS

We are most grateful to D. Azuma, Z. Bouček, and E. Grissell for their assistance in our attempts to locate the type material. The Friends of Lomas Barbudal offered logistic support for this research. The California Agricultural Experiment Station provided financial support for most of the field work. We also thank J. Oswald who offered the use of his scanner and computer during the final phase of preparing the illustrations, and two reviewers (J. Noyes and J. LaSalle) for suggesting improvements in the text.

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